Selected Aspects of Common Tern Reproductive Biology.

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ABSTRACT

Several factors influencing reproductive success were investigated at a Common Tern colony at Port Colborne, Ontario in 1976. In general three egg clutches hatched better than two egg clutches and early started clutches hatched eggs and fledged chicks better than late clutches; the fledging success of two and three egg clutches was similar. Early clutches took longer to hatch and hatched more synchronously than did late clutches. While hatching success differed with nesting substrate used fledging success did not. No relationship was found between either incubation attentiveness and reproductive success or between incubation attentiveness and clutch size. At no time did food availability appear to be a factor limiting the successful upbringing of two chick broods. While 'C' chicks (i.e. chicks hatching from the last laid eggs of three egg clutches) generally survived and grew poorly relative to their brood mates they grew best when they originated from clutches that hatched relatively asynchronously.

ACKNOWLEDGEMENTS

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INTRODUCTION

The Common Tern (*Sterna hirundo*) is a colonial ground nesting seabird belonging to the family Laridae. In North America the Common Tern breeds in both insular and non-insular habitats (see Hunter, 1976; p. 16 for review) principally in colonies along the east coast, the St. Lawrence and Great Lakes region, and in north-central U. S. A. and midwestern Canada (Austin, 1953). Common Terns often nest with a variety of other larid species (Borodulina, 1966; Langham, 1968; Cooper *et al*., 1970; Hatch, 1970; Nisbet, 1975) but in the Great Lakes their principal nesting associates are Ring-billed Gulls (*Larus delawarensis*) and Herring Gulls (*Larus argentatus*) (Ludwig, 1962; Morris, Hunter and McElman, 1976).

From wintering areas along the coastlines of Central and South America Common Terns that breed in the Northern Hemisphere migrate up the east and west coasts of North America and arrive on the nesting grounds as early as April (Palmer, 1941; Austin, 1953). After a short period of courtship and nest site selection (Palmer, 1941; Nisbet, 1973) egg laying takes place. A shallow depression is usually made in sand, gravel, or vegetated substrates or nests are made in natural depressions such as amongst rocks (Borodulina, 1966; Hunter, 1976). Two or three eggs comprise the normal clutch and each egg is laid at intervals of from one to three days (Langham, 1968; Nisbet and Cohen, 1975).

Incubation of the eggs begins sometime during the egg laying period (Borodulina, 1966; Langham, 1968; Lemmetyinen, 1973; Nisbet and Cohen, 1975) and continues right up to the time the last egg hatches. Under ideal conditions when predator (Nisbet and Cohen, 1975; Nisbet, 1975) or human disturbance (Chestney, 1970) is not evident eggs usually take from 20 to 23 days to hatch (Nisbet and Cohen, 1975) and, in general, clutches started early in the nesting season take longer to hatch and hatch more synchronously than clutches started later in the nesting season (Nisbet and Cohen, 1975; see also MacRoberts and MacRoberts, 1972; Parsons, 1972).

Hatching of the entire clutch normally takes from one and a half to three days to occur (Lemmetyinen, 1973; Nisbet and Cohen, 1975) and the chicks, once hatched, are brooded for several days thenceforth (Langham, 1972; LeCroy and Collins, 1972; LeCroy and LeCroy, 1974). Chicks are usually fed live minnows but insects and other invertebrates are known to occur in the diet (Palmer, 1941; Borodulina, 1966; Hays et al., 1972; Vermeer, 1973; Nisbet, 1973); by about 23 days of post hatch age most chicks have fledged (LeCroy and LeCroy, 1974).

The research in this thesis concerns itself primarily with particular factors which could influence the overall reproductive success of the Common Tern. My original objectives were to study reproductive success as it was influenced by differences in times of clutch initiation, differences in clutch size, differences in nesting substrate, differences in degree of attentiveness to incubation and differences in seasonal food availability. After working in the field for a short while I became particularly interested in the significance of different hatching patterns and decided to add an investigation of this phenomenon to the overall programme. As a result this thesis is presented in two parts: Part I: Factors influencing the reproductive success of Common Terns and, Part II: The significance of hatching pattern.

Numerous authors have previously assessed the reproductive success of Common Terns with regard to clutch size and time of clutch initiation (Langham, 1968; Lemmetyinen, 1973; Hunter, 1976; and Morris, Hunter and McElman, 1976). These studies generally agree that hatching success was best for three egg clutches initiated early in the breeding season. While these authors also agreed that the fledging success (i.e. chicks fledged per egg hatched) was highest early in the nesting season there was some disagreement as to whether two or three egg clutches were more successful in this regard. The fledging success of two and three egg clutches did not differ in studies by Hunter (1976) and Morris, Hunter and McElman (1976) yet LeCroy and Collins (1972) found that chicks survived best from two egg clutches. Hunter (1976) reported one case in which the fledging success of three egg clutches was better than that for two egg clutches. Egg loss also varied amongst these studies although disappearance (or predation in some studies), desertion and cracking seemed to be the most common causes of egg loss (Langham, 1968; Switzer _et al_., 1971). In addition to these, failure to hatch (Lemmetyinen, 1973), flooding (Morris, Hunter and McElman, 1976) and rotting (Hunter, 1976) were other major causes of egg loss. The causes of chick loss again varied with the different studies although most agreed that the greatest proportion of chick loss occurred within the first week after hatching (Langham, 1968; LeCroy and Collins, 1972; Lemmetyinen, 1973; Hunter, 1976) and that this mortality was mostly due to starvation, predation and/or death due to exposure during inclement weather.

Very little information is available in the literature concerning the reproductive success of Common Terns nesting on different substrates. Swickland (1974) reported that a sand substrate spread over a salt flat nesting area resulted in both increased nest density and increased hatching success for a Least Tern (*Sterna albifrons*) colony in southern California. Hunter (1976) also found that there was a difference in reproductive success (i.e. hatching success) dependent upon the nesting substrate used by Common Terns. However neither of these authors offered any explanation as to why these differences in reproductive success with nesting substrate occurred.

While several investigators have attempted to relate incubation attentiveness to reproductive success in Black-headed Gulls (Ytreberg, 1956), Black-tailed Godwits (Lind, 1961) and Herring Gulls (Baerends *et al*., 1970; Haymes, 1977) no extensive investigation of this relationship has been done for Common Terns. Preliminary investigations by Morris and Hunter (1976) did, however, suggest that there could be a relationship between reproductive success and the level of incubation attention maintained in Common Terns.

A much used procedure for establishing whether food is a factor affecting reproductive success is to artificially increase brood sizes. Under these conditions if the parent birds are regularly able to raise larger-than-normal broods to fledging then it is assumed that food is not a limiting factor. Studies of this kind done with Kittiwakes (Coulson, 1959; cited in Lack, 1966), Glaucous-winged Gulls (Vermeer, 1963), Gannets (Nelson, 1964), Black-backed Gulls (Harris and Plumb, 1965), and Herring Gulls (Haymes, 1977) all have shown that food availability was not an important factor affecting reproductive success in these species during the times and in the areas these studies were performed;

no such study has been reported for the Common Tern.

Considerable attention by Langham (1972), Nisbet (1973), LeCroy and LeCroy (1974) and Nisbet and Cohen (1975) has been given to the significance of hatching pattern in the Common Tern. All of these authors observed that the last chick to hatch in three chick broods did not survive as well as did their brood mates. Langham (1972) attributed this lower survival to the fact that as third eggs hatch last in the clutch sequence these chicks may be at some disadvantage in competing for food with older and bigger brood mates. Thus the survival of chicks hatching last in a clutch sequence may be relatively low when the age differences within the brood are great. Based on this assumption and as a possible explanation for the low fledging success of third hatching chicks late in the nesting season Nisbet and Cohen (1975) found that as the season progressed intraclutch hatching tended to be more asynchronous and as a result the age differences between chicks at hatching increased. Nisbet (1973) and LeCroy and LeCroy (1974) added that this competitive inferiority of the third hatching chick could be compounded by the fact that chicks hatching last in three egg clutches often hatched from smaller eggs and thus were relatively small individuals to begin with.

According to Lack (1966, 1968) the tendency towards asynchronous hatching late in the season is an adaptation to an irregular food supply. If food is scarce the later hatching chicks of the clutch are usually outcompeted for food by their older and bigger brood mates. Thus doomed to starve anyway, little food is wasted on those smaller chicks which usually die very soon after hatching. While investigations of similar seasonal changes in hatching pattern have been observed in

Black-backed and Herring Gulls (MacRoberts and MacRoberts, 1972; Parsons, 1972) the exact mechanisms responsible for these affects are not well known. Several supposed causes include; 1) late nesting birds begin to incubate their eggs sooner (Nisbet and Cohen, 1975), 2) early nesting birds desert their nests nocturnally during the early portion of incubation (Drent, 1970) and 3) incubation patch development is slow in early nesting birds facilitating a situation where incubation is inefficient during the egg laying period (Beer, 1962).

METHODS

Site description:

The study site was located on a man-made breakwall in Lake Erie approximately 1/2 km offshore from Port Colborne, Ontario. Several portions of the breakwall and associated rock pile were chosen as study areas for various experiments (Figure 1). Information on nesting and clutch size distribution in these areas is shown in Table 1; a description of the substrate and cover in the areas is as follows:

Area 1 was a 67 m^2 area of gravel (i.e., small, smooth stone of homogeneous size and shape) with a few scattered pieces of driftwood and an occasional boulder.

Area 2 was a 68 m^2 area of large and small rock such that nowhere was the surface flat.

Area 3 was a 97 m^2 area of broken concrete. Small chips of concrete overlaid the concrete wall to a depth of from 1 to 9 cm. Several small plants including the following grew there: *Cirsium palustre*, *Nepeta cataria*, *Avena fatua*, *Bromus sp.*, *Chenopodium sp.*, and *Senecia sp.*

Area 4 was a 180 m^2 area of concrete with a broken surface similar to area 3. Unlike area 3 however there was very little chipped rock and virtually no vegetation present.

Collection of demographic data:

Daily visits were made to areas 1, 2 and 3 from 26 April to 12 August, 1976 to collect demographic data. New nests were marked each day and the status of older eggs was noted. When the chicks began to hatch the study areas were fenced using chickenwire

Figure 1: Location of study areas used in 1976

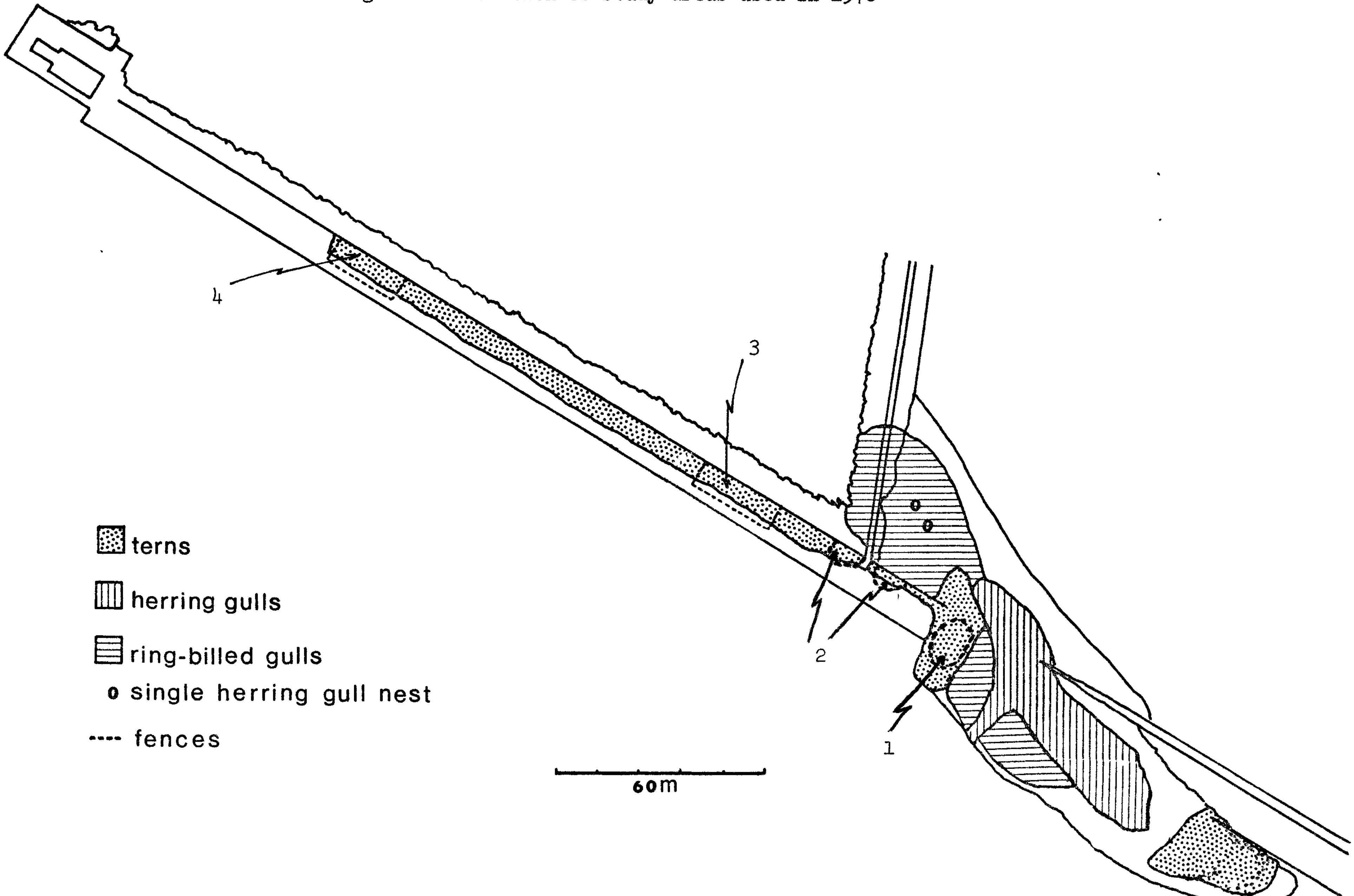


Table 1 - Information on nesting and clutch size distribution for the different study areas

Area	Substrate type	Area enclosed (m^2)	First nest started	50% egg production	90% egg production	---- Clutch size distribution ----- (# clutches) 1	2	3	4	5
1	gravel	58	26 April	5 May	15 June	16	7	35	1	0
	sand	7	27 April	9 May	17 June	3	5	13	0	0
2	rock	60	28 April	17 May	29 June	2	10	19	0	0
	sand	6	27 April	14 May	25 June	4	5	14	0	0
3	vegetated concrete	97	26 April	14 May	29 June	31	45	88	2	0
4	concrete	180	28 April	--- not determined ---						

(cf. Nisbet and Drury, 1972). Chicks were leg banded using U.S. Fish and Wildlife incoloy bands within 24 hours of hatching and all chicks were weighed every day or second day thenceforth. The sequence in which an egg was laid in a clutch, the sequence in which the egg hatched, the fate of eggs that did not hatch as well as the fate of chicks was determined as closely as possible. Chicks were considered fledged if they reached 19 days of post hatch age.

Substrate manipulation:

To facilitate testing of the effect of nesting substrate on subsequent reproductive success, 0.43 m^2 wooden boxes (n=17) filled with sand were placed in roughly a checkerboard pattern in area 1 while 13 such sandboxes were placed in a similar manner in area 2. All sandboxes were recessed into the host substrate so that the box edges were inconspicuous; all boxes were in place before the terns began to nest. Standard demographic data as described in the previous section were collected.

Incubation attentiveness:

In areas 1, 2, and 3, one, two and/or three event recorders (20-pen Esterline Angus, Model A620X) were used to record an on-nest or an off-nest event for incubating birds. Connected to the event recorders by varying lengths of insulated lamp cord were specially designed microswitch-and-arm monitoring devices (cf. Morris and Hunter, 1976) which were used at the nest. From 9 May to 30 July 44 nests were monitored for 10 days per nest between the time the clutch was completed to the time the first egg hatched while 15 nests were monitored from the time the first egg was laid until the first chick hatched. To determine whether the monitoring devices had any adverse effects on the incubating birds being monitoring, both monitored and unmonitored nests were observed simultaneously for two hours at a time. Standard demographic data as described previously was collected for those nests that were monitored.

Brood manipulations:

To determine the extent of food availability and the ability of parent birds to feed their young and how these aspects changed with season, brood manipulations were performed in area 4. From 11 June to 19 July all three egg clutches which hatched at least 2 eggs within area 4 (n=32) were individually fenced (within a 1 m radius of the nest site) and cover in the form of rocks and/or driftwood were supplied at each nest site. Clutches which hatched at least 2 eggs were chosen because these clutches can be assumed to represent the efforts of experienced breeders and a homogeneous sample of good tern parents was required for this experiment. By individually fencing each nest site as well as supplying each brood with cover I hoped to eliminate the chance of chicks wandering away from the nest site and as a result getting lost or killed, and to eliminate the chance of wandering chicks being fed by any parent other than their own. Tern chicks from nests several hundred metres distant from area 4 were added to each brood so that each brood was comprised of 5 or 6 chicks. An effort was made to ensure that the ages of the transplanted chicks corresponded closely to the age of the second hatching chick in the host brood and chicks were transplanted between the hatching of the second and third egg of the host brood. If within seven to ten days of the transplant any chicks (i.e. either host or transplant) died or disappeared a second introduction was performed to restore the brood number to five or six. After six or seven days post hatch of the third egg reintroductions were so unsuccessful that further attempts were suspended and the parent birds were assumed to have as many chicks as they could feed and care for.

Each day the broods were checked for chick fatalities and every day or every second day all chicks were weighed. To gain some insight into the species, weight and size of fish fed to chicks, regurgitated fish and fish found on the nesting substrate were identified, measured and weighed.

Statistics used:

Several non-parametric tests were used to analyze the data including 2x2 Chi Square Contingency tests corrected for continuity (X_c^2), Fisher Exact probability test (F), Kolomogorov-Smirnov test (K_d), Mann Whitney U test (U), and the Median test (X_c^2 or F) (Siegel, 1956). Because the first two tests in this list were used so often they have been identified in the text as X_c^2 and F; all other tests are specified. One parametric test was used to compare variances, slopes, and elevations (F tests) between regression lines on chick growth rates (Snedecor and Cochran , 1967). Measures of central tendency were arithmetic means and standard errors.

RESULTS

Part I: Factors influencing the reproductive success of Common Terns

Nest start and clutch size distribution:

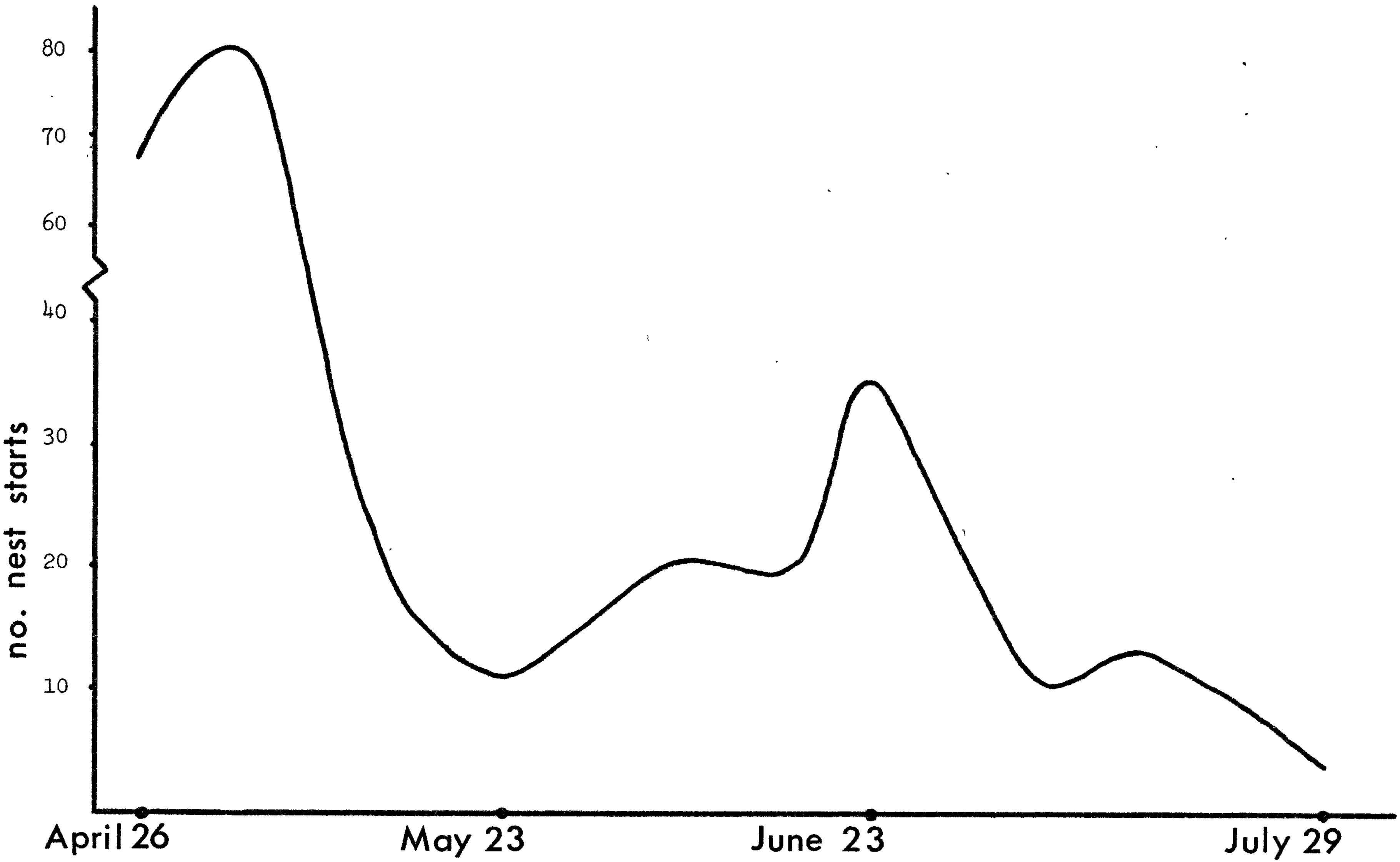
Figure 2 shows the nest start distribution of all Common Tern nests studied during 1976. The first nest was initiated on 26 April; nest starts in all study areas were initiated within 48 hours of this date. Fifty percent of the season's total egg production was present by 13 May, while 90% was present by 30 June; data for the individual study areas are presented in Table 1. The last clutch was initiated on 29 July.

The first egg hatched on 19 May. Fifty percent of the season's total hatch was present by 3 June, while 90% was present by 14 July.

In order to examine changes in reproductive success with time of nest start and at the same time maintain adequate sample sizes for testing I divided the season into an 'early' and 'late' nesting portion. On the basis of a roughly 50/50 division of the data into early/late portions I chose 23 May as the 'split date'. Henceforth 'early' shall refer to any clutch initiated before 23 May and 'late' will refer to any clutch initiated on or after 23 May. It should be understood that the split date chosen is an arbitrary one; its purpose is simply to facilitate testing of seasonal trends in reproductive success.

Within my study areas I encountered 56 cases where only one egg seemed to comprise the entire clutch (distributed 19, 6 and 31 in areas 1, 2, and 3 respectively). Of these 56 eggs only 2 hatched (3.6%) while 29 (51.8%) were deserted, 9 (16.1%) disappeared, 9 (16.1%)

Figure 2: Nest starts in all study areas combined during 1976 (including many starts for nests not subsequently analyzed in this thesis)



were fatally cracked, and 7 (12.5%) failed due to addling or embryonic mortality. One of the two chicks that hatched fledged, the other disappeared.

On the other hand, I found only 3 four egg clutches in my study areas (1 in area 1, 2 in area 3). Of these 12 eggs 8 hatched, the other 4 failed due to addling, cracking, death while pipping and investigator error. Five of the 8 chicks that hatched fledged, the other 3 were found dead.

All other clutches found contained either two or three eggs. Considering the lack of success of one egg clutches and the rarity of four egg clutches I intend to refrain from any further mention of these clutch sizes and instead concentrate subsequent analysis on two and three egg clutches.

Reproductive success and time of clutch initiation:

Hatching success according to time of clutch initiation is shown in Table 2. Early clutches consistently hatched better than late clutches and the difference was significant in 4 of 10 instances (Appendix 1). Tables 3 and 4 show egg losses according to time of clutch initiation. For two egg clutches desertion was the most common reason eggs did not hatch both early and late in the nesting season. For three egg clutches disappearance was the major cause of egg loss early in the season while cracking was the major cause late in the season.

Table 5 shows fledging success (i.e. number of chicks fledged per egg hatched) with time of clutch initiation. Early clutches consistently fledged more chicks per egg hatched than late clutches and the difference was significant in 3 of 8 cases (Appendix 2).

Table 2 - Hatching Success of Two and Three Egg Clutches In Study Areas 1, 2 and 3.

Time Period	Area 1						Area 2						Area 3		
Substrate Type	Gravel			Sand			Rock			Sand			Vegetated		
	Clutch Size (n)*	# hatch	hatch per Lay	Clutch Size (n)	# hatch	hatch per Lay	Clutch Size (n)	# hatch	hatch per Lay	Clutch Size (n)	# hatch	hatch per Lay	Clutch Size (n)	# hatch	hatch per Lay
Early	2(4)	4	1.0	2(4)	0	0.0	2(4)	3	0.75	2(2)	0	0.0	2(44)	31	0.70
	3(93)	74	0.80	3(33)	25	0.76	3(39)	32	0.82	3(39)	20	0.51	3(177)	115	0.65
Late	2(10)	3	0.30	2(6)	0	0.0	2(16)	6	0.38	2(8)	2	0.25	2(46)	10	0.22
	3(12)	5	0.42	3(6)	5	0.83	3(18)	11	0.61	3(3)	2	0.67	3(87)	33	0.38

* total number eggs laid

Table 3: Egg loss according to clutch size during the early nesting period

	area 1				area 2				area 3		all areas	
substrate type:	gravel		sand		rock		sand		vegetated		all areas	
clutch size:	2	3	2	3	2	3	2	3	2	3	2	3
# hatched	4	74	0	25	3	32	0	20	31	115	38	266
# not hatched	0	19	4	8	1	7	2	19	13	62	20	115
addled	0	5	0	1	0	1	0	3	2	6	2	16
disappear	0	2	0	1	0	1	0	10	1	17	1	31
cracked	0	2	0	3	1	0	2	4	0	12	3	21
DWP[1]	0	1	0	0	0	2	0	0	2	1	2	4
deserted	0	6	4	3	0	0	0	0	4	10	8	19
FTH[2]	0	3	0	0	0	2	0	1	4	13	4	19
error	0	0	0	0	0	1	0	1	0	3	0	5

[1] died while pipping

[2] embryo developed but died before pipping

Table 4: Egg loss according to clutch size during the late nesting period

	area 1				area 2				area 3		all areas	
substrate type:	gravel		sand		rock		sand		vegetated		all areas	
clutch size:	2	3	2	3	2	3	2	3	2	3	2	3
# hatched	3	5	0	5	6	11	2	2	10	33	21	56
# not hatched	7	7	6	1	10	7	6	1	36	54	63	67
addled	2	0	0	0	1	1	1	0	3	7	7	8
disappear	1	0	4	0	4	1	0	1	4	12	13	14
cracked	0	1	0	1	0	2	1	0	14	23	15	27
DWP[1]	0	0	0	0	0	0	0	0	0	2	0	2
deserted	4	0	2	0	3	0	4	0	12	5	25	5
FTH[2]	0	6	0	0	2	3	0	0	0	3	2	9
error	0	0	0	0	0	0	0	0	3	2	1	2

[1] died while pipping

[2] embryo developed but died before pipping

Table 5 - Fledging Success of Two and Three Egg Clutches in Study Areas 1, 2 and 3

Time Period	Area 1						Area 2						Area 3		
Substrate Type	Gravel			Sand			Rock			Sand			Vegetated		
	Clutch Size (n)*	# fledge	Fledge per hatch	Clutch Size (n)	# fledge	Fledge per hatch	Clutch Size (n)	# fledge	Fledge per hatch	Clutch Size (n)	# fledge	Fledge per hatch	Clutch Size (n)	# fledge	Fledge per hatch
Early	2(4)	2	0.50	2(0)	-	-	2(3)	3	1.0	2(0)	-	-	2(31)	24	0.77
	3(74)	52	0.70	3(25)	17	0.68	3(32)	28	0.88	3(20)	18	0.90	3(115)	62	0.54
Late	2(3)	0	0.0	2(0)	-	-	2(6)	5	0.83	2(2)	0	0.0	2(10)	5	0.50
	3(5)	0	0.0	3(5)	0	0.0	3(11)	2	0.18	3(2)	2	1.0	3(33)	14	0.42

* total number hatch

An analysis of fledging success on a fledge-per-egg-laid basis (Table 6) also revealed that early clutches fledge chicks better than late clutches and the difference was significant in 5 of 10 instances (Appendix 3). Figure 3 and 4 show that the majority of chicks which died or disappeared did so within 3 days of hatching both early and late in the season.

Reproductive success and clutch size:

Table 2 shows that with two exceptions the hatching success of three egg clutches exceeded that of two egg clutches and the difference was significant in 2 of 10 cases (Appendix 4). Where statistically feasible early and late data were pooled and whole season comparisons of two *vs* three egg clutches were made. In two cases a significant difference was found; in both cases three egg clutches hatched significantly better than two egg clutches (area 1, sand substrate: $X^2_c = 16.73$, $p < .001$ and area 2, rocky substrate: $X^2_c = 4.95$; $.01 < p < .05$). When two and three egg clutches were compared with regard to egg loss (Tables 3 and 4) it was found that both early and late two egg clutches had significantly more eggs deserted than did early and late three egg clutches (early: $X^2_c = 4.50$; $.01 < p < .05$, and late: $X^2_c = 17.22$; $p < .001$); no other significant differences were found.

Fledging success (i.e. fledge peregg hatch) according to clutch size is shown in Table 5. While these results showed that neither clutch size was consistently more successful two egg clutches were found to fledge chicks more successfully than three egg clutches when these data were tested statistically (Appendix 5). Because no significant

Table 6 - Reproductive Success of Two and Three Egg Clutches In Study Areas 1, 2, & 3.

Time Period	- Area 1 -						- Area 2 -						- Area 3 -		
Substrate Type	Gravel			Sand			Rock			Sand			Vegetated		
	Clutch Size (n)*	# fledge	fledge per lay	Clutch Size (n)	# fledge	fledge per lay	Clutch Size (n)	# fledge	fledge per lay	Clutch Size (n)	# fledge	fledge per lay	Clutch Size (n)	# fledge	fledge per lay
Early	2(4)	2	0.50	2(4)	0	0.0	2(4)	3	0.75	2(2)	0	0.0	2(44)	24	0.55
	3(93)	52	0.56	3(33)	17	0.52	3(39)	28	0.72	3(39)	18	0.46	3(177)	62	0.35
Late	2(10)	0	0.0	2(6)	0	0.0	2(16)	5	0.31	2(8)	0	0.0	2(46)	5	0.11
	3(12)	0	0.0	3(6)	0	0.0	3(18)	2	0.11	3(3)	2	0.67	3(87)	14	0.16

* total number eggs laid

Figure 3: Chick disappearance and death with chick age during the early nesting period (April 26 - May 23) for all study areas combined.

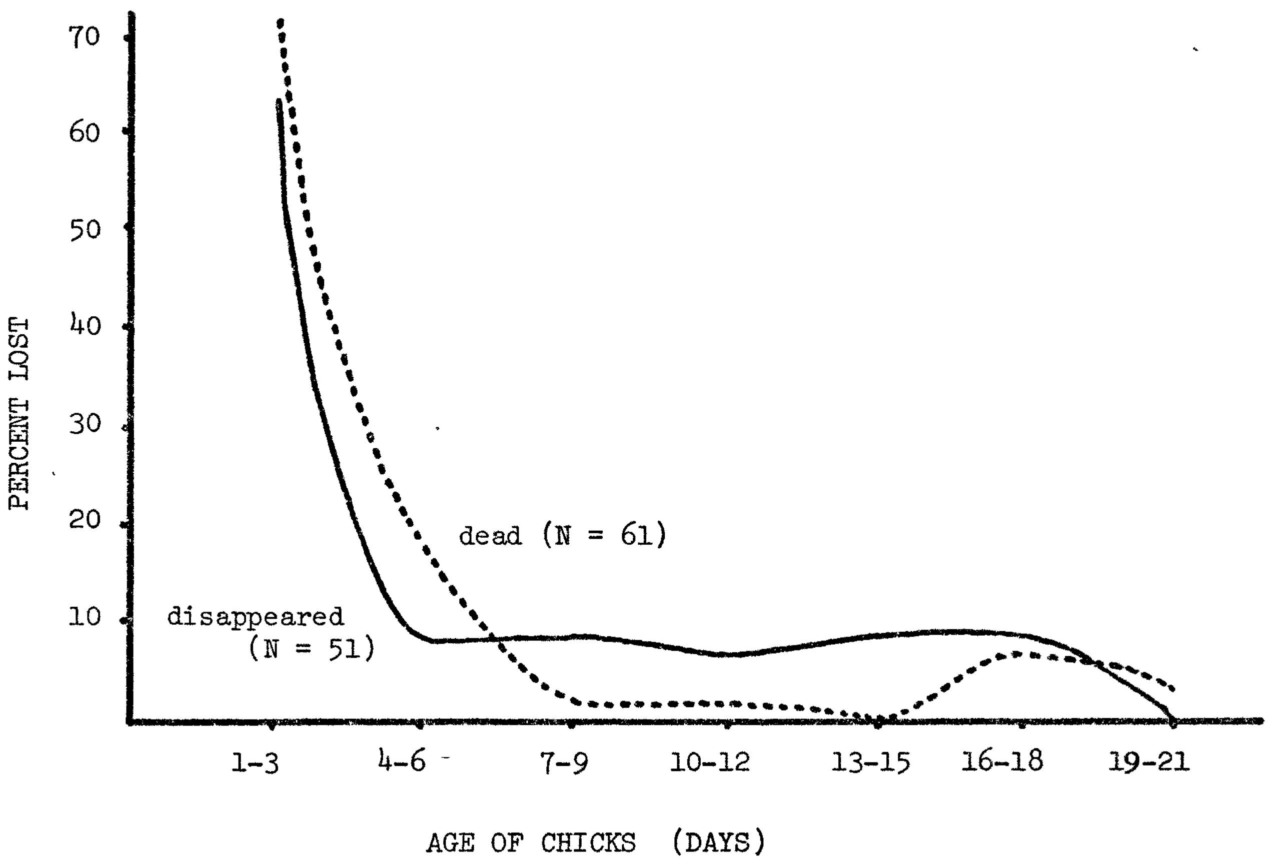
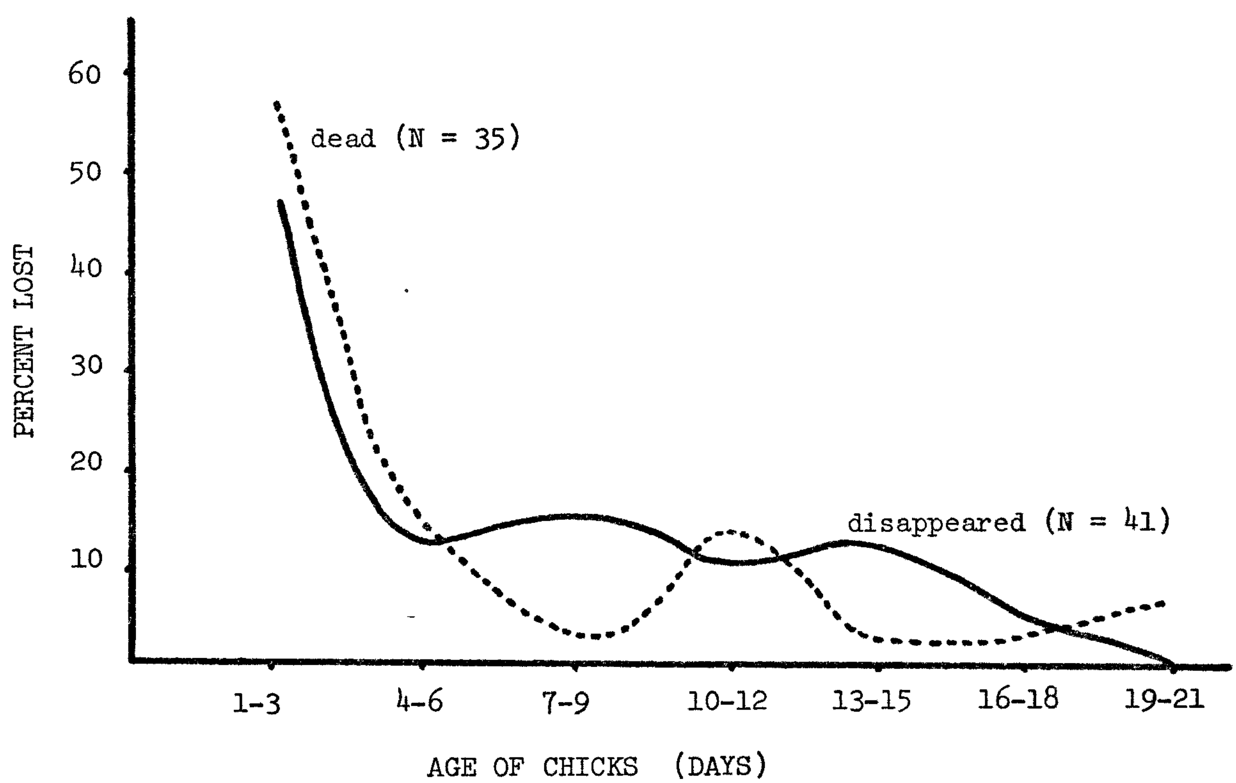


Figure 4: Chick disappearance and death with chick age during the late nesting period (May 24-July 28) for all study areas combined.



difference was found between area 3 early and late two and three egg clutches these data were pooled and a whole season comparison was made. Again two egg clutches fledged significantly more chicks per egg hatched than did three egg clutches ($X_c^2 = 4.13$; $.01 < p < .05$). When fledging success was analyzed on a fledge-per-egg-laid basis (Table 6) similar results were obtained and 1 of 10 cases showed that two egg clutches fledged significantly more chicks per egg laid than did three egg clutches (Appendix 6). Conversely, a whole season comparison of the area 2, sandy substrate data showed that three egg clutches fledged significantly more chicks per egg laid than two egg clutches ($X_c^2 = 7.06$; $.001 < p < .01$).

Reproductive success and nesting substrate:

Hatching success on different nesting substrates is shown in Table 2. Eggs usually did not hatch as well on sand as on the host substrates and the difference was significant in 2 of 8 cases (Appendix 7). Where pooling was statistically feasible whole season comparisons were made and one further case of a significant difference was found; three egg clutches laid in area 2 hatched significantly better on rock than on the sand ($X_c^2 = 4.73$; $.01 < p < .05$). When egg loss was examined (Tables 3 and 4) two cases of a significant difference between substrates were found; early two egg clutches laid in area 1 were deserted more often on sand than on gravel ($F = .01$) and on a whole season basis, three egg clutches disappeared significantly more often in area 2 from sand than from rock ($F = .04$).

No clear trends were found with regard to fledging success and nesting substrate on a fledge-per-hatch basis (Table 5) and no significant differences were found (Appendix 8). On a fledge-per-egg-laid basis it was found that fledging was usually better on the host substrates than on the sand (Table 6) and the difference was significant in 1 of 8 cases (Appendix 9).

Reproductive success and incubation attention:

To determine whether the monitors had any adverse effects on those nests that were monitored hatch, fledge and reproductive statistics for monitored and unmonitored nests were examined (Table 7). These data indicate no significant differences between monitored and unmonitored three egg clutches. Furthermore a total of 38 nest hours was spent observing 10 monitored and 9 unmonitored nests. Birds spent an average of 58.3 minutes/hour on monitored nests and 57.8 minutes/hour on nests that were not monitored. In all the cases I observed that incubating birds habituated to the monitors within 10 minutes and that normal incubation ensued from that point forward. These results suggest that the monitors caused no undue distress to the birds.

Before examining the relationship between incubation rate and subsequent reproductive success I first had to resolve an inconsistency in my data. For the majority of nests I had only collected 10 days of incubation data. This did not prove to be an analysis problem for those cases in which no eggs were lost and at least one egg hatched because the average incubation rate calculated over 10 days tended to agree very closely with the incubation rate for one day of incubation (see Figure 7 and section on factors contributing to hatching pattern - Part II). However, in those cases where one or more eggs were lost from the nest the incubation rate was found to vary

Table 7 - Reproductive statistics for monitored[1] and unmonitored three egg clutches

	Monitored	Not Monitored
# eggs laid	72	78
# eggs hatch per egg laid	0.65	0.64
# chicks fledge per egg hatch	0.49	0.50
# chicks fledge per egg laid	0.32	0.32

1. Monitoring devices (cf. Morris & Hunter, 1976) were placed at each nest.

considerably depending on the juxtaposition of egg loss and the period when incubation data was collected (Table 8). For this reason I decided to consider cases where eggs were lost only when I had data for the whole incubation period, the rationale being that in order to make the comparisons I wished to make I first had to ensure that all data were consistent in their representation of the whole incubation period and thus were comparable. On completion of this operation I categorized the average incubation rates according to substrate, clutch size, time of clutch initiation and hatching (Appendix 10) and fledging (Appendix 11) success. Because this categorization fragmented the data so badly and because the trends in incubation appeared to be consistent over all the substrates I pooled the data for the substrates (Tables 9 and 10) so that I could better assess the relationships between hatching and fledging success and incubation attention.

While hatching success did not appear to be related to the level of incubation attention, those clutches which lost one or more (but not all) eggs usually were incubated less on average than clutches that lost no eggs (Table 9). Table 8 showed a number of cases where an egg was lost during incubation and for which I had information on incubation rates before and after egg loss. In 6 of 7 cases these data showed that egg loss depressed subsequent incubation rate. However it is obvious that egg loss had a number of different effects. Egg loss could result in a depressed incubation rate which might lead to desertion (as in case 2 and 3) or which could lead to further egg loss (as in case 5) or which might have no further detrimental effect (as in case 1 and 7). On the other hand

Table 8: Egg loss and its effect on incubation rate and reproductive success

case #	clutch size	egg laying	min./hr. spent on nest over three day period[1] (# hours analyzed)						egg fates
1	3	55.57 (54)	57.24 (38)	59.04 (24)	58.72 (25)	57.22 (51) *	56.21 (58)	53.52 (58)	#1 disappear #2 hatch #3 hatch
2	3	57.21 (58)	57.08 (28)	57.53 (19) *	53.53 (53)	50.88 (24)	desertion		
3	3	47.75 (60)	54.49 (47)	56.53 (49) *	46.88 (41)	desertion			
4	3	57.30 (37)	58.76 (34)	59.14 (50)	59.20 (51)	58.86 (57) *	59.08 (52) *	59.19 (54)	#1 disappear #2 crack #3 hatch
5	3	41.44 (50)	53.30 (44) *	48.60 (10)	52.43 (44)	47.42 (43) *	50.81 (53)	28.74 (27) *	all disapp.
6	3	52.83 (42)	55.51 (47)	58.79 (56) *	54.87 (39)	55.85 (35)	57.94 (17) **		all disapp.
7	2	no data	55.84 (45)	55.11 (45)	55.34 (58)	56.66 (58) *	49.93 (54)	51.00 (23)	#1 hatch #2 disappear

* represents the loss of an egg from the nest

[1] all periods of 3 days duration except the first (egg laying) and the last in each case

Table 9: The relationship between hatching success and incubation attention for all study areas combined.

% time spent on the nest	3 egg clutches # eggs hatch 3	2	1	0	2 egg clutches # eggs hatch 2	1	0
			EARLY PERIOD				
95-100	7	5	0	0	3	3	0
90-95	0	0	0	0			
80-90	0	0	1	0			
70-80	0	0	0	0			
			LATE PERIOD				
95-100	4	7	3	0	7	0	0
90-95	1	0	1*	0	3	0	0
80-90	0	1*	0	1*	0	1*	0
70-80	0	0	0	0	0	0	1*
60-70							1*

* clutches that lost one or more eggs and whole incubation period is considered; ten days of incubation period considered when clutches lost no eggs.

Table 10 - The relationship between fledging success and incubation attention for all study areas combined.

% time spent on nest	3 egg clutches number fledge				2 egg clutches number fledge		
	3	2	1	0	2	1	0
				EARLY PERIOD			
95 - 100	1	7	4	0	2	4	0
90 - 95	0	0	0	0			
80 - 90	0	0	1	0			
				LATE PERIOD			
95 - 100	0	0	0	14	2	1	4
90 - 95	0	0	0	2*	0	0	3
80 - 90	0	0	1*	1*	0	0	1*
70 - 80					0	0	1*
60 - 70							1*

* clutches that lost one or more eggs and whole incubation period is considered; ten days of incubation period considered when clutches lost no eggs.

egg loss could have no effect on incubation rate (as in case 4) or it could only temporarily depress the incubation rate (as in case 6).

There also did not appear to be a relationship between the level of incubation attention and fledging success (Table 10). While in 9 of 10 late clutches that were incubated less than 95% of the time no chicks were fledged (6 of the 9 clutches hatched at least 1 egg), 18 of 21 late clutches that were incubated more than 95% of the time also did not fledge any chicks (21 clutches hatched at least one egg).

Reproductive success and food availability:

To establish the effect of adding chicks to broods the fledging success of native and transplanted chicks was analyzed (Table 11). These data show that although more native chicks fledged than did initially introduced chicks the difference was not significant ($X^2_c = 2.20$; $p > .05$). However, second introductions of chicks fledged significantly more poorly than did either native ($X^2_c = 22.28$; $p < .001$) or initially introduced chicks ($X^2_c = 12.86$; $p < .001$).

The fledging success of manipulated broods with time of clutch initiation and hatching success of the host brood is shown in Table 12. These results show that early broods fledged more chicks on average than late broods even though early and late broods hatched chicks just as successfully and were manipulated in the same way. That early broods fledged 4 and 5 chicks suggests that food availability was not limited during the early nesting period and that the ability of the parent pair to raise larger than normal broods was not limited. If the ability to raise large broods was also not an inherent limitation

Table 11 - Fledging success of chicks from Manipulated broods according to the resident status of the chick

Resident Status	Native[1]			Initial Introduction[2]			Second Introduction[3]		
	# chicks	# fledge	fledging success[4]	# chicks	# fledge	fledging success[4]	# chicks	# fledge	fledging success[4]
	79	45	.57	86	38	.44	40	4	.10

1. chicks hatched from manipulated clutch
2. chicks added to manipulated clutch from other clutches
3. same as 2 only these were chicks which were added after some chicks from the original introduction had died or disappeared.
4. number of chicks fledged per total number of chicks in that category.

Table 12 - Number of chicks fledged[2] from manipulated broods according to time of clutch initiation and clutch size.

Time of clutch initiation	clutch size	hatching case	number broods	number chicks added[1]	number chicks fledge					
					5	4	3	2	1	0
Early	3	3	5	3	1	3	1	0	0	0
Late	3	3	3	3	0	0	2	1	0	0
	3	3	11	2	0	0	6	4	0	1
	3	2	13	3	0	0	9	4	0	0

1. number of chicks added to bring total brood size to 5 or 6.

2. reaching 19 days of post hatch age

of parent pairs nesting later in the season then the fact that late nesting pairs did not raise large broods suggests that food availability was limited at that time. Assuming these relationships were true I compared the growth and fledging weights of unmanipulated 2 and 3 chick broods from nests initiated early in the breeding season (i.e. presumably not food stressed as larger manipulated broods were successfully raised) with the growth and fledging weights of the manipulated broods. The purpose of this analysis was to determine if the manipulated broods would show a depressed growth rate and lower fledging weights as a result of food stress.

To measure chick growth the average chick weight gain of the brood between the 7th and 15th day post hatch was used; day 7 was used as the earliest age because chick growth up to this time was disrupted due to reintroductions. Because the death of chicks during this 7 to 15 day period probably effected the growth of chicks in that brood all such broods where this occurred were eliminated from the analysis. Fledging condition was measured as the average chick weight of the brood for the period following 20 days of post hatch age (in previous analyzes '19 days' was used as the earliest fledge date because this was the age when chicks first began to escape from the study areas. Strictly speaking chicks did not begin to fledge until about 21 days post hatch and thus for analysis in this section, where weight at fledging is important as an indicator of post fledging survival, '21 days' post hatch is used instead of '19 days'). The results of this analysis (Table 13) show that chicks from manipulated late broods fledging three chicks grew at the same rate and fledged at similar weights as did manipulated early broods fledging more than three chicks. However growth and fledging in the manipulated broods which fledged three or more chicks appeared to be depressed

Table 13 - Average growth and fledging weights of chicks from manipulated and unmanipulated broods.

	Time of Clutch Initiation	chick N*	weight gain age 7-15 days $\bar{x}$	SE	chick N*	fledge weight at 20+ days $\bar{x}$	SE
Manipulated #fledge/brood							
5	early	5	49.8	3.10	5	117.2	1.43
4	early	12	50.1	1.94	12	119.7	1.18
3	late	34	46.9	2.02	31	120.1	2.18
2	late	14	56.6	3.02	14	120.6	1.41
Unmanipulated							
3	early	57	58.1	0.93	39	120.6	0.72
2	early	44	56.1	1.45	53	122.0	1.07

* # chicks considered

** at least two weights per chick beyond age 20 days were required before the chick was included (weights were averaged) when compared with the unmanipulated early broods fledging three chicks; growth of chicks in manipulated broods fledging 3 and 4 chicks was significantly lower than growth of chicks in unmanipulated broods fledging 3 chicks ($X^2_c = 13.83$; $p < .001$ and $X^2_c = 4.93$; $.01 < p < .05$ (Median Tests) respectively).

If, as the previous analysis shows, growth rates of manipulated broods were depressed because of food stress then these growth rates should be good indicators of food availability. To arrive at an estimate of how food availability varied with season total brood weight gain (i.e. sum of weight gains of individual brood member between 7 and 15 days of post hatch age) was used. The broods were then grouped according to the correspondence of the 7 to 15 day chick age intervals with calendar positions so that the groups of broods represented a seasonal progression. In each of these groups the brood weight gains were summed and divided by the number of broods (i.e. mean brood weight gain). These weight gains, used as estimates of food availability (Figure 5) suggest that food availability decreased as the season progressed until very near the end of nesting when food availability increased again.

Table 14 shows the number, lengths (mouth to tail fin tip) and weights of fish species taken by Common Terns. Assuming my sampling method was random the numbers, lengths and weights found are probably representative of at least the relative proportions of each species taken. Of most noteworthy mention with regard to these data is the predominance of emerald shiners and rainbow smelt in the diet of early nesting terns while in the late nesting period there was a very heavy reliance on troutperch.

Figure 5: Changes in seasonal food availability as measured by average brood weight gain between day 7 and 15 post hatch

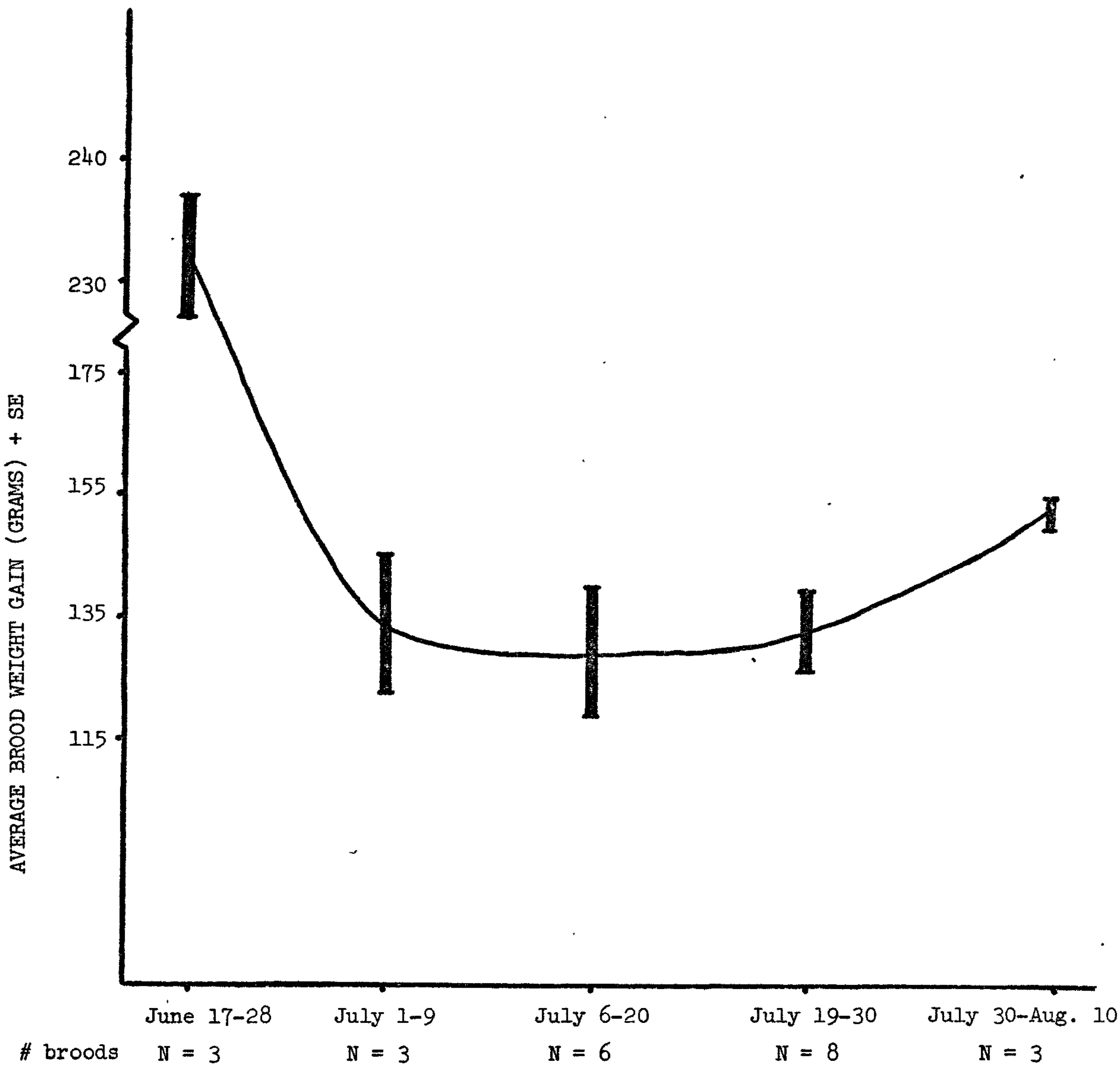


Table 14: Fish found in the nesting area or regurgitated by Common Terns

Nesting period fish were found	Species	average length (N) (mm)	range	average weight (N) (g)	range
Early	emerald shiner (*Notropis atherinoides*) Rafinesque	90.4(10)	83-96	4.9(4)	4.8-5.0
	rainbow smelt (*Osmerus mordax*) Mitchell	115 (9)	74-162	6.9(5)	2.5-11.6
	trout perch (*Percopsis omiscomaycus*) Walbaum	103.5(4)	63-121	13.2(2)	12.9-13.4
	northern fathead minnow (*Pimephales promelas*) Rafinesque	66.5(2)	61-72	3.0(2)	2.0-3.9
	northern logperch (*Percina caprodes*) Rafinesque	96 (1)	--	6.3(1)	--
Late	trout perch	89.3(22)	71-127	5.3(13)	1.9-13.0
	rainbow smelt	125 (3)	108-136	7.9(3)	5.6-10.3
	emerald shiner	80 (3)	62-94	3.2(3)	1.6-4.1
	fathead minnow	90 (1)	--	6.0(1)	--
	common shiner (*Notropis cornutus*) Mitchell	110 (1)	--	8.2(1)	--

DISCUSSION

Part I: Factors influencing the reproductive success of Common Terns

Reproductive success with clutch size and time of clutch initiation:

Although the different study areas used in this study encompassed a wide variety of substrate types and varied positionally with regard to the rest of the colony and to nesting heterospecifics (i.e. Herring and Ring-billed Gulls) certain trends in reproductive success were common throughout. For example, hatching and fledging success of two and three egg clutches was in no instance significantly better later in the nesting season than earlier, however the reverse was true in numerous instances. Equally common was that three egg clutches hatched significantly better than two egg clutches; in no case did two egg clutches hatch significantly better than three egg clutches. Finally, chicks that died or disappeared did so with greatest frequency before four days of post-hatch age. In general these results agree with studies done by Langham (1968), LeCroy and Collins (1972), Lemmetyinen (1973), Hunter (1976) and Morris, Hunter & McElman (1976) for Common Terns. In contrast considerable variation was found regarding fledging success according to clutch size. The fledging success of two and three egg clutches was not significantly different according to Morris, Hunter and McElman (1976) and in some instances in this study. Numerous cases of a significantly better fledging success for two egg clutches have been reported by LeCroy and Collins (1972) and in this study; one case of better fledging success of three egg clutches is reported in this study and one has been reported by Hunter (1976). LeCroy and Collins (1972), the only authors to comment on these data, believed that the higher fledging success of two egg clutches reflected in part the greater survival chances of the fewer chicks the smaller clutch size produced.

This study showed that for three egg clutches disappearance was the major cause of egg loss early in the season while cracking was the major cause later in the season. For two egg clutches desertion was the major cause of egg loss both early and late in the nesting season. Although Langham (1968), Hunter (1976) and Morris, Hunter & McElman (1976) did not look at egg loss with regard to clutch size, for all clutches combined they found that disappearance and desertion were major egg loss categories and cracking was variable in importance. That this study reported that two egg clutches were deserted significantly more often than three egg clutches could have been due either to the fact that the two egg clutches were actually three egg clutches which lost an egg and this resulted in desertion (cf. Table 8) or to the fact that more two egg clutches than three egg clutches belonged to inexperienced, sick and/or undernourished individuals who were unable to lay a third egg and/or were unable to hatch and raise young at this time (cf. Lack, 1966; Langham, 1968).

Differences in reproductive success with nesting substrate:

To determine whether there were any differences in reproductive success as a result of nesting substrate sand was introduced into nesting areas comprised of gravel and rocky substrates in such a way as to form a patchwork of sand and natural nesting substrates. Comparisons of reproductive success were then made between the sand and the substrates they were host to.

In no case did two or three egg clutches hatch significantly better on the sand substrate than they did on the host, however the reverse was true in two instances. Only one of these cases was credible in terms of an ample sample size; early three egg clutches hatched significantly better on the rock substrate than on the sand. One reason for the poor hatching success on the sand may have been that eggs were more visible to predators especially on the rock hosted sand since these substrates contrasted especially strongly. In support of this hypothesis it was found that eggs from three egg clutches disappeared significantly more often from the sand than they did from the rocky substrate. In apparent contradiction of this Hunter (1976), who performed this same experiment at this same colony in 1973, found that during the late nesting period sand-based three egg clutches had a significantly higher hatching success than rock-based three egg clutches ($X^2_c = 11.05$; $p < .001$).

Neither Hunter nor I found any significant differences in fledging success between the substrates when two and three egg clutches were examined separately for the early and late periods.

Clearly the results of this study and that of Hunter's suggest that differences in nesting substrate can have a marked effect on reproductive success, primarily on hatching success.

Differences in reproductive success with incubation attention:

The fact that I did not find a relationship between incubation levels and hatching and fledging success either early or late in the nesting season does not mean that such a relationship does not exist as overall rates of incubation may be relatively unimportant to the final hatching outcome. What may be critical to successful hatching is that incubation be assiduous at certain times during incubation. Adverse weather conditions such as driving rain (Skutch, 1957; Rittinghaus, 1961), particularly low air temperatures (Lind, 1961) and particularly high air temperatures (Drent, 1975; p. 358) may require that the bird incubate very closely to prevent egg damage. More assiduous incubation may also be critical later on in incubation when the developing embryos become more and more sensitive to temperature as hatching approaches (MacMillan and Eberhardt, 1953; Moreng and Bryant, 1956; Howell and Bartholomew, 1962; Hunter et al., 1976).

Incubation studies concerning several gull species suggest that the level of incubation attentiveness is dependent on the number of eggs present in the nest (Beer, 1965; Baerends et al., 1970). Three egg clutches elicit the optimum incubation response presumably because of the complete tactile stimulus three eggs supply to the incubating bird when the three eggs accommodate three incubation patches on the abdomen of the bird (Beer, 1965). Conversely clutches of smaller or larger size transmit inadequate or confusing tactile stimuli which may cause the incubating bird to rise and settle more often and which may otherwise elicit suboptimum incubation responses (Beer, 1965 ; Baerends et al., 1970). As Baerends has suggested, these suboptimum incubation responses may be responsible for higher rates of predation in one, two and four egg clutches of the Herring Gull.

In disagreement with the above findings I found that Common Terns incubated two egg clutches just as assiduously as they did three egg clutches. Furthermore I would disagree with the conclusions Baerends drew concerning the relationship of clutch size and incubation levels with predation rate. In Baerends' study one, two and four egg clutches were obtained by adding to or reducing three egg clutches. According to my results with Common Terns this experimental procedure would have caused a depression of the incubation rate which in turn could have been responsible for further egg loss (cf. Table 8). With this perspective I am prompted to suggest that the predation rates in Baerends' study were due to the clutch manipulations and not directly to clutch size. Furthermore, if the tactile stimulus theory were correct, then when three egg clutches are reduced to two egg clutches a permanently reduced incubation rate should occur. Contrary to this hypothesis, however, is evidence that the incubation rate is depressed only temporarily in these cases and that with gradual habituation to the new clutch arrangement incubation rate may regain its former high level (Table 8, case 6; Lind, 1961; p. 128).

Food availability and reproductive success late in the nesting season:

It should not be too surprising to find that Common Terns can successfully raise supranormal broods to fledging in the light of similar results obtained with Kittiwakes (Coulson, 1959; cited in Lack, 1966: p. 245-247), Glaucous-winged Gulls (Vermeer, 1963), Gannets (Nelson, 1964), Herring Gulls (Haymes, 1977) and Lesser Black-backed Gulls (Harris and Plumb, 1965). At least for Common Terns in this study this ability was limited to early in the breeding season and as one might have expected both growth and fledging weight of chicks in these supranormal broods was inferior to growth and fledging weights of chicks in normal sized broods during the same time period.

If the indirect method used to calculate food availability in this study is correct in its representation food was not a major factor limiting the upbringing of a normal sized brood late in the season. That fledging of two and three chicks occurred consistently during the late part of the nesting season tends to support this contention (cf. Table 12). Although growth of chicks in late broods which fledged three chicks did show signs of depressed growth the fledging weights of these chicks were normal.

If not due to food scarcity then there are two alternatives which could explain the lower reproductive success experienced by late nesting birds. One possibility could be the predominance of younger, less experienced individuals breeding during this time (cf. Austin, 1938; 1940; Lack, 1966; p. 240-245; Langham, 1968; p. 53). I believe the following evidence tends to confirm this. From twenty-three late started clutches in study areas 3 and 4 which were not manipulated and which hatched at least two chicks per clutch the fledging rate (i.e. fledge per hatch) was 54.72%. Similarly fifty-three early started clutches in study areas 3 and 4 which hatched at least two chicks per clutch had a fledging success of 59.84%. Assuming these groups generally comprised the older, more experienced individuals the important difference is that these groups comprised 55% and 22% respectively of nests started in the early and late nesting periods.

Another possible reason for a decreased overall reproductive success late in the season given that there was no substantial food shortage was increased predation. In area 1, which bordered on Herring and Ring-billed Gull nesting areas, no chicks fledged from nineteen late started clutches in which at least two chicks hatched per clutch. Furthermore 100% of these chicks disappeared before fledging. In contrast, in area 1 thirty-seven early started clutches from which at least two chicks hatched per clutch the fledging success was 68.26% with 57.58% of the chick losses being due to disappearance. Because I saw no other predators present (cf. Hunter, 1976; p. 114-118) I believe that Ring-billed and Herring Gulls were responsible for most of the disappearance of Common Tern chicks. Although I did see signs of Herring Gull predation on Common Tern chicks the damage did not seem to be as extensive as that reported by Hatch (1970) who estimated that the annual toll of Common Tern chicks taken by Herring Gulls may be as high as 0.48 - 1.2 chicks per adult tern pair. Inconsistent with this supposition, however, is that predation should occur mostly later in the season yet Ring-billed and Herring Gulls were present throughout the whole season. One possible explanation for this is that later in the season fledgling gulls were doing much of the predation as fledging only began late in the season (i.e. around June 20). Another explanation is that the greater tern nesting density present early in the season facilitated a more effective predator defense and thus deterred predation by the gulls more so than did the dispersed late nesting terns (cf. Darling, 1938; Kruuk, 1964).

RESULTS

Part II: The significance of hatching pattern

Factors contributing to variation in hatching pattern:

While working in the field I noticed that the hatching pattern of early nesting terns tended to be very synchronous relative to late nesting terns whose hatching pattern was relatively asynchronous. A subsequent analysis of this situation (Table 15) confirmed these observations. Because this effect could have been due to differences in egg laying intervals I tabulated early and late egg laying intervals (Table 16). This analysis showed that the average interval (in days) between laying of the first and second, the second and third, and the first and third was slightly greater for early clutches (1.73 vs 1.65; 1.98 vs 1.83; 3.71 vs 3.51 respectively) suggesting that the laying interval did not contribute to the difference in hatching synchrony between early and late clutches. To determine whether there were any differences in the quality of incubation between these two periods I plotted levels of incubation with day of incubation (Figure 6). But for the period from the time the first egg was laid until four days after clutch completion the early and late incubation rates were similar. To establish whether there were differences in the early incubation stages which could have accounted for the differences in hatching synchrony I plotted the number of days eggs of three egg clutches took to hatch on a seasonal scale (Figure 7). This plot showed that early eggs took longer to hatch than late eggs, the difference being most acute prior to laying of the second egg. This suggests that the level of incubation attentiveness in early clutches was relatively

Table 15: Degree of hatching synchrony in three egg clutches[1] with time of clutch initiation as measured by between-visit[2] hatching.

Time of Clutch Start	3 eggs hatch between visits		2 eggs hatch between visits		1 egg hatches between visits	
	#[3]	%[4]	#[3]	%[4]	#[3]	%[4]
Early	2	3.3	35	58.3	23	38.3
Late	0	0	2	22.2	7	77.8

1. only clutches where the number eggs hatched = the number of eggs laid is considered.

2. visits were made every 24 hours.

3. number of clutches where condition occurred.

4. percentage of clutches in which condition occurred.

Table 16: Egg laying intervals for three egg clutches with time of clutch initiation.

Time of Clutch start	Early #clutches	%	Late # clutches	%
Egg #1&2 # of days between laying:				
1	30	32.3	30	35.7
2	58	62.4	53	63.1
3	5	5.4	1	1.2
Egg #2&3 # of days between laying:				
1	23	24.7	24	28.6
2	49	52.7	50	59.5
3	21	22.6	10	11.9
Egg #1&3 # of days between:				
2	5	5.4	4	4.8
3	31	33.3	41	48.8
4	46	49.5	32	38.1
5	8	8.6	6	7.1
6	3	3.2	1	1.2

Figure 6: Characterization of incubation with day of incubation and time of clutch initiation.
(only three egg clutches where no eggs were lost are included in this analysis)

[1] refers to number of hours analyzed

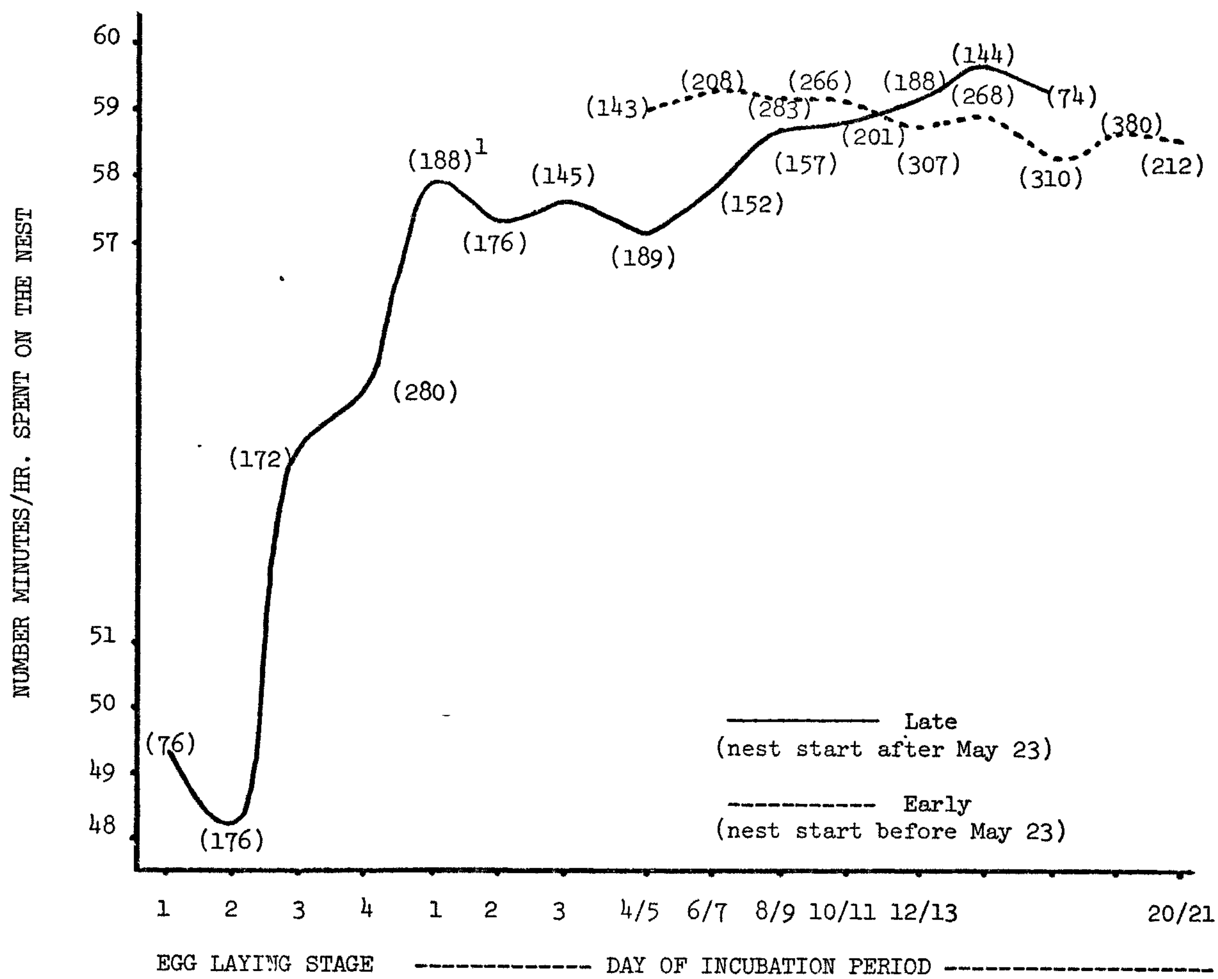
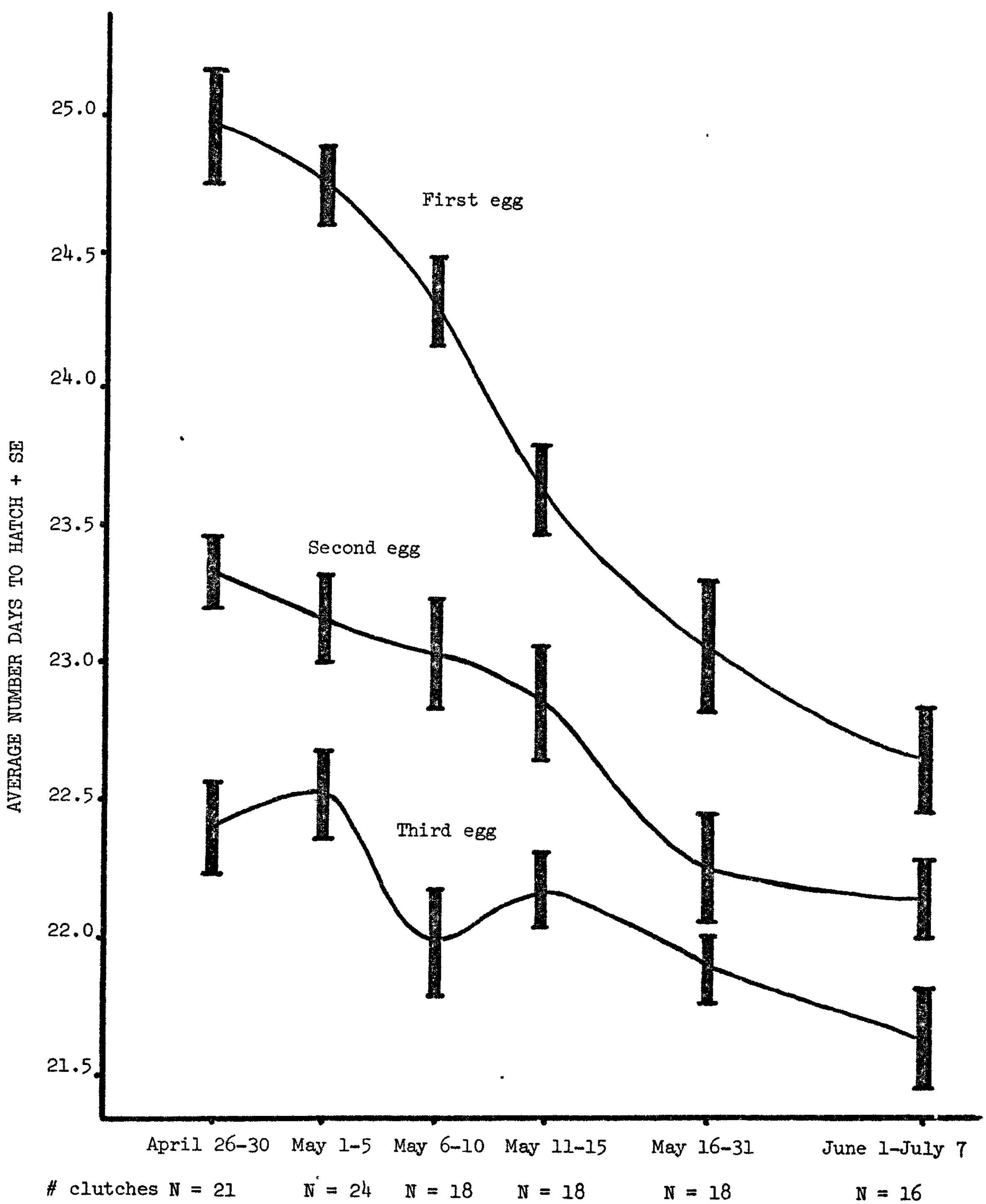


Figure 7: Average number of days to hatch of the eggs of three egg clutches with time of nest start



low in the initial stages of incubation, and especially low prior to laying of the second egg. The relatively greater delays in hatching of the first and second eggs of early clutches would explain how these eggs, that were laid several days apart, could come to hatch so close together.

Chick growth and survival with sequence of hatching:

To determine what effects different hatching patterns could have on subsequent chick growth and survival I analyzed chick growth and fledging success according to egg number and sequence of hatching. To facilitate identification of which chick hatched from what egg the following nomenclature shall henceforth be used:

The first laid eggs in three egg clutches shall be referred to as 'A' eggs; the chicks hatching from these eggs shall be referred to as 'A' chicks. Eggs laid second in the sequence and chicks hatching from these eggs shall be referred to as 'B' eggs and chicks, and third laid eggs and chicks hatching from these eggs shall be referred to as 'C' eggs and chicks. With the exception of the case where A and B eggs hatched between visits to the colony (i.e. sequence of hatching unknown) all eggs in the following analysis hatched in the order in which they were laid.

To obtain two groups of clutches which had different hatching patterns yet did not differ in any other respect I selected only three egg clutches which were initiated early in the nesting season. Broods which fledged three chicks were categorized as either 'synchronous' (syn) if the first two chicks hatched between visits to the colony (i.e. within a 24 hour period) or 'asynchronous' (asyn) if they did not. This categorization was inescapable but fortunately provided me with two groups with significantly different hatching patterns (overall hatching intervals: 1.64 $\pm$ .20 days (syn) vs 2.30 $\pm$ .15 (asyn); U = 26; N = 11, 10; p = .05, Mann Whitney U Test). In other respects such as nest start distribution (K_d = 2; N = 10; p > .05, Kolmogorov-Smirnov Test), overall egg laying interval (3.27 $\pm$ .27 (syn) vs 3.20 $\pm$ .29 (asyn); U = 52; N = 11, 10; p > .05), and hatching and fledging weights (Table 17) the groups did not differ significantly.

To assess growth and fledging success of two chick broods, three egg clutches which fledged only two chicks were analyzed.

To analyze chick growth the following procedures were used:

1) Chicks were put into groups on the basis of what egg they hatched from and how many other chicks fledged from their brood.

2) Three egg clutches which fledged only two chicks were examined if i) three eggs hatched but one chick died so soon after hatching that the growth rate of the other two chicks could not have been appreciably affected, ii) two eggs hatched and one did not.

3) Only growth between the ages of four and fifteen days inclusive was analyzed because this portion of the growth phase was very linear; only chicks weighed at least five times during this growth interval were considered.

4) A linear regression technique correlating chick weight with post hatch age was used to classify chick growth. To reduce variation and to standardize the regressions each sample weight for a given chick was divided by the hatching weight of that chick.

5) The variances, slopes and elevations of the regression lines were compared using F tests (see Snedecor and Cochran , 1967; p. 432-436).

Table 17: Inter- and intrabrood differences in hatching and fledging weights of three chick broods as revealed by statistical analysis.[1]

Group	chicks compared	hatching pattern	mean hatch weight (g)	SE	# broods considered	U	mean fledge weight[2] (g)	SE	# broods considered	U
a	A	asyn	15.80	.51	10	39.5 NS	122.11	2.10	9	36.5 NS
	B	"	16.40	.43	10		122.67	2.57	9	
b	B	"	16.40	.43	10	34.5 NS	122.67	2.57	9	32.5 NS
	C	"	15.40	.54	10		123.88	1.48	8	
c	A	"	15.80	.51	10	43.5 NS	122.11	2.57	9	26.5 NS
	C	"	15.40	.54	10		123.88	1.48	8	
d	A & B	"	16.10	.33	20	211 NS	122.39	1.61	18	196.5 NS
	A & B	syn	16.23	.29	22		122.86	1.51	22	
e	C	asyn	15.40	.54	10	51 NS	123.88	1.48	8	32.5 NS
	C	syn	15.55	.36	11		122.09	1.27	11	

1. Mann Whitney U Test (u)

2. Day 21 post hatch taken as earliest fledge date.

Appendix 12 shows the results of regressions done on the chick groups. All regressions yielded a high degree of correlation between chick age and growth ($p < .001$ in all cases).

The results of an intra- and interbrood analysis of chick growth in three chick broods is presented in Table 18; these results can be summarized as follows:

1) In asynchronous hatching broods B chicks grew significantly better than C chicks (group b). However growth rates of A and B chicks and A and C chicks were not significantly different (groups a and c respectively).

2) Growth of C chicks from asynchronously hatching broods was significantly better than growth of C chicks hatching from synchronous hatching broods (group e).

3) Because the growth rates of A and B chicks of asynchronous hatching broods were not significantly different (group a) these data were pooled and then compared with the combined growth rates of A and B chicks of synchronous hatching broods (group d); no significant differences were found.

An analysis of hatching and fledging weights of chicks in two chick broods revealed no significant differences (Table 19). The results of an intra- and interbrood analysis of chick growth in two chick broods is presented in Table 20; these results can be summarized as follows:

1) Growth of chicks in A and B and in A and C chick broods did not differ significantly (group f and g respectively).

2) In B and C chick broods the variances were too heterogeneous to allow a statistically valid comparison of slopes and elevations (group h).

Table 18: Intra- and interbrood comparison[1] of chick growth in three chick broods as revealed by regression analysis.

Group	chicks compared	hatching pattern	# broods considered	F tests[2] variance homogeneity	slope	elevation
	A	asyn	10	1.12	1.98	3.63
a	B	asyn	10			
	$\boxed{B}$	asyn	10	1.55*	1.35	4.04*
b	C	asyn	10			
	A	asyn	10	1.39	0.33	2.73
c	C	asyn	10			
	A & B combined	asyn	10	1.18	0.38	1.77
d	A & B combined	syn	11			
	C	syn	11	1.03	1.35	7.33**
e	$\boxed{C}$	asyn	10			

1. regression anova information in Appendix 12.
2. Snedecor & Cochran , 1967; p. 432-436.

$\square$ had the significantly greater growth

* $.01 < p < .05$

** $p < .01$

Table 19: Inter- and intrabrood differences in hatching and fledging weights of two chick broods as revealed by statistical analysis.[1]

Group	chicks compared	brood composition	mean hatch weight (g)	SE	# broods considered	U	mean fledge weight[2] (g)	SE	# broods considered	U
f	A	A, B	15.25	.25	8	20 NS	118.17	5.62	6	16 NS
	B	A, B	14.88	.52	8		121.67	3.30	6	
g	A	A, C	14.89	.56	9	36 NS	119.25	2.39	8	24 NS
	C	A, C	14.78	.36	9		120.50	2.62	8	
h	B	B, C	15.56	.63	9	22.5 NS	121.00	1.73	8	34 NS
	C	B, C	14.33	.44	9		122.00	2.01	9	
i	A	A, C	14.89	.56	9	32 NS	119.25	2.39	6	23.5 NS
	A	A, B	15.25	.25	8		118.17	5.62	8	
j	B	A, B	14.88	.52	8	26.5 NS	121.67	3.30	6	21.5 NS
	B	B, C	15.56	.63	9		121.00	1.73	8	
k	C	A, C	14.78	.36	9	34.5 NS	120.50	2.62	8	31.5 NS
	C	B, C	14.33	.44	9		122.00	2.01	9	
1	A	A, C	14.89	.56	9	31 NS	119.25	2.39	8	24.5 NS
	B	B, C	15.56	.63	9		121.00	1.73	8	

1. Mann Whitney U Test (u). 2. day 21 post hatch taken as earliest fledge date.

Table 20: Intra- and Interbrood comparison of chick growth[1] in two chick broods as revealed by regression analysis

				F tests[2]		
Group	chicks compared	brood composition	# broods considered	variance homogeneity	slope	elevation
f	A	A, B	8	1.06	0.76	0.05
	B	A, B	8			
g	A	A, C	9	1.56	0.98	0.04
	C	A, C	9			
h	B	B, C	9	2.61**	--	--
	C	B, C	9			
i	$\boxed{A}$	A, C	9	1.13	2.21	8.73**
	A	A, B	8			
j	$\boxed{B}$	A, B	8	1.48	2.45	7.03**
	B	B. C	9			
k	C	A, C	9	2.05*	--	--
	C	B, C	9			
l	A	A, C	9	1.23	1.27	0.76
	B	B, C	9			

1. for regression anova information see Appendix 12
2. Snedecor & Cochran , 1967; p. 432-436

□ had the significantly greater growth.

* $.01 < p < .05$

** $p < .01$

3) Growth of A chicks was significantly better when their brood mates were C chicks rather than B chicks (group i).

4) Similarly growth of B chicks was significantly better when their brood mates were C chicks rather than A chicks (group j).

5) Growth of C chicks in A and C and in B and C chick broods could not be compared because the variances were too heterogeneous (group k).

6) Growth of A and B chicks was not significantly different when their brood mate was a C chick (group L).

Fledging success (i.e. fledge per hatch) of three egg clutches with sequence of hatching is shown in Table 21. These results show that C chicks did not generally survive as well as did A and B chicks; however no significant differences were found.

Table 21: Fledging success (fledge/egg hatch) of three egg clutches[1] according to egg number for all study areas combined.

	Hatch Situation				
	egg A & B hatch within 24 hours		all eggs hatched on separate days		
	Egg A & B	C	Egg A	B	C
# clutches	24			23	
# fledge	36	16	17	18	14
fledging success	.75	.67	.74	.78	.61

1. only early nests considered; only cases where all the eggs that were laid hatched are considered.

DISCUSSION

Part II: The significance of hatching pattern

Factors contributing to variation in hatching pattern:

In this study it was found that eggs from early clutches took longer to hatch than eggs from late clutches. While human interference (Chestney, 1970) and predator disturbance (Nisbet, 1973; Nisbet and Cohen, 1975) are known to delay hatching these factors could not have contributed to the observed delays in hatching of early eggs because both factors were more evident late in the season. Furthermore, a seasonal comparison of incubation attentiveness with day of incubation (cf. Figure 6) revealed that if the delays in hatching were due to incubation inattentiveness that this inattentiveness must have been confined to the early stages of incubation. In this context it is not unlikely that the early nesting terns deserted the colony nocturnally during the initial stages of incubation as this is a characteristic typical of many bird species (Beer, 1962; Kendeigh, 1952; Lind, 1961; Drent, 1970). Although this early nocturnal desertion would account for the delays in hatching of early eggs, the effects of nocturnal desertion on hatching pattern would predictably be more subtle. Other factors, having more influence on hatching pattern, might thus be expected to exist. One such factor could be that the incubation patches of the early nesting terns were slow in developing and this reduced incubation efficiency during the initial stages of incubation (cf. Beer, 1962). Birds nesting later in the season might not experience this delay in incubation patch development, especially when renesting occurred since the incubation patches may not have had time to degenerate from the previous nesting attempt.

While a combination of early nocturnal desertion and differences in incubation patch development could have accounted for the different hatching patterns of early and late nesting terns in this study what caused the more subtle differences in hatching pattern found within the early nesting period? It is possible that there was variation in the duration of nocturnal desertion (cf. Drent, 1970) and in initial incubation patch development (especially if the more asynchronous hatching clutches belonged to renesting individuals) between nesting pairs which could have caused these differences in hatching pattern. That these factors were involved is supported by the fact that A eggs took significantly longer to hatch in synchronous hatching broods ($23.55 \pm .16$ (syn) vs $22.60 \pm .27$ (asyn); $U = 20.5$, $N = 11, 10$; $.01 < p < .05$; Mann Whitney U Test) even though there was little variation in the length of time B and C eggs took to hatch between the two groups ($21.91 \pm .09$ (syn) vs $22.10 \pm .23$ (asyn); $21.55 \pm .16$ (syn) vs $21.70 \pm .21$ (asyn)). Not to discount subtle differences in egg laying intervals which my visitation rate prevented me from detecting, the observed differences in hatching intervals could also have been due to intraclutch differences in egg size (Nisbet and Cohen, 1975; Parsons, 1975) or to differences in the quality of incubation supplied to clutches during the hatching interval (Lind, 1961; Norton, 1972). While this last factor could result because of inherent differences in attentiveness between pairs, it is more likely to occur as a result of prevailing weather conditions. Norton (1972) found that when adverse weather conditions occurred just prior to and during hatching that incubation attentiveness was very assiduous and as a result hatching was asynchronous as compared with when moderate weather conditions prevailed, incubation was less assiduous and hatching more synchronous. However this latter possibility must be rejected because of the fact that the synchronous and asynchronous early broods in this study had the same nest start distribution and as such they should have been similarly affected by weather.

Chick growth and survival with sequence of hatching:

In this study it was found that C chicks generally survived and grew poorly relative to their brood mates. These results agree with those obtained by Langham (1972) who observed that the relatively late hatching of C chicks facilitated the situation where the C chick was not fed adequately because it exhibited a poor begging response relative to its older and bigger brood mates. While the poor survival and growth of C chicks may be due to sequence of hatching evidently other factors may also be involved. In an experiment with Herring Gulls Parsons (1975) interchanged A eggs which had just started pipping with pipping C eggs so that the A eggs hatched last whilst the C eggs hatched first. While the manipulated C chicks survived better than C chicks in unmanipulated clutches the manipulated C chicks did not survive as well as the manipulated A chicks which were induced to hatch last in the hatching sequence. Both Parsons' study and that of Nisbet (1973) concluded that growth and survival of C chicks could also be related to the fact that C chicks often hatch from relatively small eggs. The relatively low hatching weights of C chicks (cf. Tables 17 and 19) and the poor growth of C chicks in two chick broods (i.e. where sequence of hatching should not have been that important a factor, cf. Table 20) in this study lends support to this contention.

On the other hand, the finding that C chicks grew significantly better when they hatched from asynchronous rather synchronous hatching clutches is somewhat difficult to attribute to anything but hatching sequence as all other variables which could have influenced this result were not significantly different between the two groups compared. Assuming hatching pattern was primarily responsible for the observed differences in growth of the C chick then why did the C chick grow better in the asynchronous broods? To answer this question I examined chick ages at the time the C chick hatched in both groups and found that the interval between hatching of the B and C eggs was longer in the synchronous hatching broods (1.64 $\pm$ .20 (syn) vs 1.20 $\pm$ .13 (asyn); difference not significant). In relative terms this would mean that in the asynchronous hatching broods that C chicks would have to compete with one very much older brood mate and one not so much older brood mate while in the synchronous hatching broods the C chick at hatching would have to contend with two almost identical brood mates of intermediate age. It is therefore possible that the C chick, at hatching, finds competition for food easier in an asynchronous hatching brood because in these broods the C chick is on more equal terms with at least one other brood mate.

Hatching asynchrony has generally been accepted as an adaptation to an irregular food supply (Lack, 1966; Nisbet and Cohen, 1975) yet no one has reported on its adaptiveness in a situation of food abundance. Findings in this study suggest that food was abundant during the early nesting period (cf. Part I - section on food availability) and results in this section showed that overall chick growth was better in asynchronously hatching <u>early</u> broods than in more synchronously hatching broods of the same time period (cf. Table 18 - groups d and e). On the basis of these findings one might suggest, therefore, that 'asynchrony' is the hatching pattern best suited to Common Terns. regardless of food supply. As hatching 'synchrony' in the strictest sense is rare in Common Terns (cf. Table 15 - three eggs hatch within 24 hrs: N = 2) one might then best think of less asynchronous hatching patterns as variants of asynchronous rather than of synchronous hatching patterns.

For Common Terns an asynchronous hatching pattern is probably essential as this hatching pattern facilitates brooding care of the A and B chicks while the C egg is being hatched. As Common Tern chicks may not be fully endothermic for two or three days after hatching (LeCroy and Collins, 1972) and as high rates of chick mortality occur during this time (cf. Figures 3 and 4) it would seem necessary that brooding care be adapted for. In a very synchronous hatching situation less brooding would be possible as both parents would have to forage in order to provide enough food for themselves and for their brood.

SUMMARY AND CONCLUSIONS

Several factors influencing the reproductive success of Common Terns at a Port Colborne, Ontario ternery were investigated during the 1976 nesting season. The results of this investigation can be summarized as follows:

1) Three egg clutches initiated early in the nesting season generally experienced a higher hatching success than three egg clutches initiated late in the nesting season. In addition, three egg clutches hatched better than two egg clutches.
2) The greater proportion of chicks that died or disappeared did so before four days of post hatch age.
3) While early started clutches consistently fledged more chicks than late started clutches in many instances the fledging success (either fledge/lay or fledge/hatch) of two and three egg clutches did not differ. However, several cases of a significantly better fledging success of two egg clutches were found when the data were analyzed on a fledge-per-egg-hatch basis while only one case of a significantly better fledging success of three egg clutches was found and then only when the data were analyzed on a fledge-per-egg-laid basis.
4) Three egg clutches initiated on a rocky nesting substrate hatched significantly better than three egg clutches initiated on sand. This difference in hatching success was due to a significantly higher disappearance rate of eggs from sand-based clutches.
5) No apparent relationship between incubation attentiveness and reproductive success or between incubation attentiveness and clutch size was found. However, loss of one or more eggs from a clutch

often resulted in a depressed incubation rate which may have facilitated further egg loss or desertion of the nest.

6) While food availability did not appear to be a factor limiting the successful raising of three chick broods early in the nesting season, there did appear to be some such limitation late in the nesting season as growth of chicks in these late broods seemed to be slightly retarded.

7) A review of the literature together with an examination of circumstantial evidence prompted me to suggest that the lower reproductive success of late nesting birds was due to increased predation and to a greater proportion of younger, less experienced breeders present during the late rather than during the early nesting period.

In Part II of this thesis I examined the significance of hatching pattern in Common Terns. These results can be summarized as follows:

1) Eggs in clutches initiated early in the nesting season took longer to hatch and clutches hatched more synchronously than did eggs and clutches initiated during the late nesting period.

2) Because there did not appear to be any seasonal differences in incubation attentiveness except during the egg laying and initial stages of incubation it was concluded that the observed seasonal differences in days to hatch and in hatching synchrony were attributable to differences in the quality of incubation supplied to clutches during the initial stages of incubation. Several reasons for these seasonal differences in quality of incubation are discussed.

3) An analysis of chick growth and survival with sequence of hatching in three chick broods revealed that the 'C' chick (i.e. last chick

to hatch in the clutch) survived and grew poorly relative to its brood mates. This poor performance of the C chicks was attributed to their relatively low weights at hatching and to the fact that these chicks were the youngest chicks in the brood and thus the most vulnerable.

4) C chicks in early started clutches where the eggs hatched close together did not grow as well as did C chicks in early clutches where the eggs hatched significantly more asynchronously. Possible explanations for this result are discussed together with an evaluation of the adaptive significance of an asynchronous hatching pattern to Common Terns.

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Appendix 1: Differences in hatching success between early and late nesting birds according to study area and clutch size as revealed by statistical analysis

	Area 1				Area 2				Area 3	
Substrate Type	Gravel		Sand		Rock		Sand		Vegetated	
Clutch Size	X_c^2[1]	p	X_c^2[1]	p	X_c^2[1]	p	X_c^2[1]	p	X_c^2[1]	p
2	F[2]	0.03[3]	F[2]	ns	F[2]	ns	F[2]	ns	19.60	<.001[3]
3	6.29	<.05[3]	F[2]	ns	1.89	ns	.007	ns	16.23	<.001[3]

1. Chi square 2x2 contingency with Yates correction for continuity.
2. Fisher Exact Probability Test
3. Early nesting birds hatched significantly more eggs than late nesting birds.

Appendix 2: Differences in fledging success between early and late nesting birds according to study area and clutch size as revealed by statistical analysis.

	Area 1				Area 2				Area 3	
Substrate type	Gravel		Sand		Rock		Sand		Vegetated	
Clutch Size	X^2_c[1]	p	X^2_c[1]	p	X^2_c[1]	p	X^2_c[1]	p	X^2_c[1]	p
2	F[2]	ns	--	--	F[2]	ns	--	--	1.58	ns
3	7.39	<.01[3]	F[2]	.009[3]	15.51	<.001[3]	F[2]	ns	0.934	ns

1. Chi square 2x2 contingency with Yates correction for continuity.

2. Fisher Exact Probability Test

3. Early nesting birds fledged significantly more chicks per egg hatched than late nesting birds.

Appendix 3: Differences in reproductive success between early and late nesting birds according to study area and clutch size as revealed by statistical analysis.

	Area 1				Area 2				Area 3	
Substrate type	Gravel		Sand		Rock		Sand		Vegetated	
Clutch Size	X^2_c[1]	p	X^2_c[1]	p	X^2_c[1]	p	X^2_c[1]	p	X^2_c[1]	p
2	F[2]	ns	F[2]	ns	F[2]	ns	F[2]	ns	17.69	<.001[3]
3	<11.15	.001[3]	F[2]	.023[3]	15.84	<.001[3]	.007	ns	9.30	<.001[3]

1. Chi square 2x2 contingency with Yates correction for continuity.

2. Fisher Exact Probability Test.

3. Early nesting birds fledged significantly more chicks per egg laid than late nesting birds.

Appendix 4: Differences in hatching success between two and three egg clutches according to study area and time of clutch initiation as revealed by statistical analysis.

Substrate Type	Area 1				Area 2				Area 3	
	Gravel		Sand		Rock		Sand		Vegetated	
Time Period	X_c^2[1]	p	X_c^2[1]	p	X_c^2[1]	p	X_c^2[1]	p	X_c^2[1]	p
Early	0.133	ns	F[2]	.007[3]	.109	ns	.476	ns	0.26	ns
Late	F[2]	ns	F[2]	.008[3]	1.06	ns	F[2]	ns	2.90	ns

1. Chi square 2 x 2 contingency with Yates correction for continuity.

2. Fisher Exact Probability Test.

3. Three egg clutches hatched significantly better than two egg clutches.

Appendix 5: Differences in fledging success between two and three egg clutches according to study area and time of clutch initiation as revealed by statistical analysis.

	Area 1				Area 2				Area 3	
Substrate Type	Gravel		Sand		Rock		Sand		Vegetated	
Time Period	X_c^2 [1]	p	X_c^2 [1]	p	X_c^2 [1]	p	X_c^2 [1]	p	X_c^2 [1]	p
Early	0.900	ns	--	--	F[2]	ns	--	--	4.64	$<.05$[3]
Late	F[2]	ns	--	--	F[2]	0.017[3]	F[2]	ns	0.004	ns

1. Chi square 2x2 contingency with Yates correction for continuity
2. Fisher Exact Probability Test
3. Two egg clutches fledge significantly more chicks per egg hatched than three egg clutches.

Appendix 6: Differences in reproductive success between two and three egg clutches according to study area and time of clutch initiation as revealed by statistical analysis.

Time Period	Substrate Type	Area 1				Area 2				Area 3	
		Gravel		Sand		Rock		Sand		Vegetated	
		X_c^2 [1]	p	X_c^2 [1]	p	X_c^2 [1]	p	X_c^2 [1]	p	X_c^2 [1]	p
Early		.079	ns	F[2]	ns	.042	ns	.305	ns	4.86	$<.05$ [3]
Late		F[2]	ns	F[2]	ns	1.05	ns	F[2]	ns	0.312	ns

1. Chi square 2x2 contingency with Yates correction for continuity.

2. Fisher Exact Probability Test

3. Two egg clutches fledged significantly more chicks per egg laid than three egg clutches.

Appendix 7: Differences in hatching success with nesting substrate according to clutch size and time of clutch initiation as revealed by statistical analysis.

Area	Time Period	Substrate Type	3 egg clutches		2 egg clutches	
			X_c^2 [1]	p	X_c^2 [1]	p
	Early					
1		Gravel vs Sand	0.045	ns	F[2]	.014[3]
2		Rock vs Sand	6.981	$<.01$[4]	F[2]	ns
	Late					
1		Gravel vs Sand	F[2]	ns	F[2]	ns
2		Rock vs Sand	F[2]	ns	F[2]	ns

1. Chi square 2x2 contingency with Yates correction for continuity.

2. Fisher Exact Probability Test.

3. Gravel has significantly higher hatching success than sand/gravel.

4. Rock has significantly higher hatching success than sand/rock.

Appendix 8: Differences in fledging success with nesting substrate according to clutch size and time of clutch initiation as revealed by statistical analysis.

			3 egg clutches		2 egg clutches	
Area	Time Period	Substrate Type	X^2_c[1]	p	X^2_c[1]	p
	Early					
1		Gravel vs Sand	.001	ns	--	--
2		Rock vs Sand	.519	ns	--	--
	Late					
1		Gravel vs Sand	F[2]	ns	--	--
2		Rock vs Sand	F[2]	ns	F[2]	ns

1. Chi square 2x2 contingency with Yates correction for continuity.

2. Fisher Exact Probability Test.

Appendix 9: Differences in reproductive success with nesting substrate according to clutch size and time of clutch initiation as revealed by statistical analysis.

Area	Time Period	Substrate Type	3 egg clutches		2 egg clutches	
			X_c^2 [1]	p	X_c^2 [1]	p
	Early					
1		Gravel vs Sand	.054	ns	F[2]	ns
2		Rock vs Sand	4.29	$<.05$[3]	F[2]	ns
	Late					
1		Gravel vs Sand	F[2]	ns	F[2]	ns
2		Rock vs Sand	F[2]	ns	F[2]	ns

1. Chi square 2x2 contingency with Yates correction for continuity.

2. Fisher Exact Probability Test.

3. Nests on a rocky substrate fledged significantly more chicks per egg laid than nests on sand.

Appendix 10: The relationship between hatching success and average time spent incubating clutches for Common Terns nesting on different substrates at different times of the season.

	Substrate:	Gravel			Rocky					Vegetated						
Time Period	% time spent on nest/hr.	3-egg clutches - # hatch - -			3-egg clutches - # hatch - -			2-egg clutches - # hatch - -		3-egg clutches - # hatch - -				2-egg clutches - # hatch - -		
		3	2	1	3	2	1	2	1	3	2	1	0	2	1	0
Early	95-100	2	1	0						5	4	0	0	3	3	0
	90-95	0	0	0	- - No Data - - - - - - - - - -					0	0	0	0	0	0	0
	80-90	0	0	0						0	0	1	0	0	0	0
Late	95-100	3	3	0	1	2	1	3	0	0	2	2	0	4	0	0
	90-95	1	0	0	0	0	0	2	0	0	0	1*	0	1	0	0
	80-90	0	0	0	0	0	0	0	0	0	1*	0	1*	0	1*	0
	70-80															1*
	60-70															1*

* clutches that lost one or more eggs and whole incubation period is considered; ten days of incubation period considered when clutches lost no eggs.

Appendix 11: The relationship between fledging success and average time spent incubating clutches for Common Terns nesting on different substrates at different times of the season.

	Substrate:	Gravel				Rocky							Vegetated						
Time Period	% time spent on nest/hr	3-egg clutches - - # fledge -				3-egg clutches - - # fledge -				2-egg clutches - - # fledge -			3-egg clutches - - # fledge -				2-egg clutches - - # fledge -		
		3	2	1	0	3	2	1	0	2	1	0	3	2	1	0	2	1	0
Early	95-100	0	3	0	0								1	4	4	0	4	2	0
	90-95	0	0	0	0	- - - No Data - - - - - - - - -							0	0	0	0	0	0	0
	80-90	0	0	0	0								0	0	1	0	0	0	0
Late	95-100	0	0	0	6	0	0	0	4	0	0	3	0	0	0	4	2	1	1
	90-95	0	0	0	1	0	0	0	0	0	0	2	0	0	0	1*	0	0	1
	80-90	0	0	0	0	0	0	0	0	0	0	0	0	0	1*	1*	0	0	1*
	70-80																		1*
	60-70																		1*

* clutches that lost one or more eggs and whole incubation period is considered; ten days of incubation period considered when clutches lost no eggs.

Appendix 12: Regression information on chick growth with age.

Brood Composition	chick	slope	y-intercept	- Residuals - - SS[1]	df[2]	ms[3]	corr. coeff.	SE
A,B,C (asyn)	A	.486	.141	16.88	66	.256	.957	.506
	B	.472	.155	13.96	61	.229	.959	.478
	C	.514	-.218	21.61	61	.354	.949	.595
	A&B	.479	.145	31.27	129	.242	.957	.492
A,B,C (syn)	A&B	.475	.095	46.13	161	.287	.952	.535
	C	.480	-.144	23.16	68	.341	.942	.584
A, B	A	.457	.117	35.82	55	.651	.896	.807
	B	.464	-.044	36.03	52	.693	.898	.832
B, C	B	.523	-.168	22.97	49	.469	.941	.685
	C	.531	.028	8.84	49	.180	.975	.425
A, C	A	.502	.206	31.76	55	.577	.918	.760
	C	.521	-.095	19.93	54	.369	.950	.607

1. SS = sum of squares

2. df = degrees of freedom

3. ms = mean square

Appendix 13: Definitions of reproductive parameters used in this thesis.

Hatching success - the number of eggs hatched per egg laid

Fledging success - the number of chicks fledged per egg hatched

Reproductive success - the number of chicks fledged per egg laid.

* Some confusion may arise in the text of this thesis because of this latter definition because I often use the term 'reproductive success' in the general sense to mean all of the parameters defined above.